SOME POINTS ON CLEAVAGE AMONG ARTHROPODS.

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In the development of an animal from the egg to the hatched form one great problem has always to be met. That problem lies in the development of a multicellular animal from a unicellular element. For every egg is in its essential structure of this simple type—it is composed of a cell-body and nucleus. Other modifications in the form of membranes, shells, envelopes of any kind and even food material or yelk are secondary. Since all animals, with the exception of certain plant-like forms and unicellular organisms, develop from eggs, there is in the course of development of every individual this great transition from a single-celled egg to a many-celled adult.

Details of the processes by which this transition takes place are many and varied within the wide limits of the animal kingdom, but the same principle controls the process throughout. The means by which the single-celled egg becomes a multicellular structure are known under the general name of cleavage. The egg divides into two parts, which may be equal or not, varying with different kinds of eggs. The subsequent division of each of these parts into two and these again into two increases the number of cells in the developing egg in geometrical ratio, the ultimate result being a many-celled embryo, having eventually the many tissues and organs that compose the adult body.

While the process can in general be called by the same name, "cleavage," in all types of animal life, there are many fundamental differences in the details and comparing extreme cases it is difficult to see how the varied methods found can be in any way connected. However, the existence of very different methods of cleavage among closely related forms of animals demands the bridging of these gaps and the clear understanding of transitions from one type to another. In ultimate analysis, these differences in the first stages of development are found to depend on a single fact, which may be stated briefly as the amount of food material or yelk present in the egg in proportion to its size. This is the key to the law which controls the early form of the superstructure, as it rises by the process of cleavage.

The greatest variation, within close limits, seems among the large sub-kingdom of invertebrate animals, and among the invertebrates no class offers a more interesting and profitable field of study than the Arthropod, including as it does insects, myriapods, crustaceans, spiders. Among the crustaceans many forms of cleavage are found. Some of the lower groups show the most primitive type, the eggs being holoblastic in their cleavage. In this process the egg is cut directly into two equal or approximately equal parts, which again divide and their products divide until a mass of equal or approximately equal cells result. Each cell contains a nucleus surrounded by some cystoplasm and some food material or yelk. The method of forming a multicellular animal from a unicellular egg in such a case is, in its early stages, controlled by a single law—that of cell-division, sometimes equal, sometimes unequal; but cells of the early stages arise by complete division of the egg and those of the latter by complete division of the preëxisting cells. This kind of cleavage is found to occur only in those eggs having a small amount of equally distributed yelk or food material. This in turn limits it to eggs of a small size and nearly or quite spherical form.

Passing now to the Insecta, the highest of the Arthropods, very different conditions are found to prevail. The eggs of most of the Insecta are larger in proportion to the size of the animal than among crustaceans, contain more yelk and are usually either oval, disc-like or curved-rod-shaped. The result of all these modifications is to greatly modify the kind of cleavage. Instead of any such process as has been described, the centrally placed nucleus divides repeatedly with no division of the surrounding yelk mass, which is placed in meshes of an extremely attenuated network of protoplasm. The nuclear division proceeds on exactly the same principle as that on which the whole egg segments in the holoblastic cleavage. This continues until a large group of nuclei has been formed in the middle of the egg (Fig. 1). These nuclei, owing, in part at least, to their increasing number, migrate toward the surface of the egg and eventually form a uniform layer of nuclei over the surface, imbedded in a rather thick layer of protoplasm that has always covered the egg surface. Finally, cell outlines appear between the nuclei and a blastoderm, one cell in thickness is formed, enclosing yelk, as yet uncleaved. At the end of blastoderm formation, however, the nuclei are not all in a peripheral position, a certain number are scattered equally through the yelk. Later, the yelk breaks up into a number of masses, in the center of each being a nucleus, one of those previously scattered through the yelk. This secondary yelk cleavage, as it is known, is the retarded expression of holoblastic cleavage, the only point in the development of such an egg that suggests the simple holoblastic type. This, then, is the typical form of cleavage among insects, nuclear and protoplasmic division, leaving the yelk mass intact until a late stage.

There is a group of insects very lowly in their organisation that have been as yet but incompletely studied, even by the systematist. These, the Apterygota by name, form a large group of mostly small wingless insects, remarkable for their generalised characters. The commonest and most familiar of this group is Lepisma or the "silver fish," wellknown for its destructive habits in eating paste from the book-bindings and other similar acts. Although the systematic zoologist has subdivided the whole group into well-marked sub-groups and many different species are recognised, yet the embryology has remained for a long time untouched, with the single exception of a few observations of surface changes. With the increase in nicety of microscopical technique and improvements in the microscope, the difficulties of handling and studying eggs of extremely small sizes and delicate composition have been so reduced that a careful study of the minute eggs of members of the group Apterygota is now possible.

It has been my privilege to undertake an investigation into the embryological development of *Anurida maritima*, a small member of this group, widely scattered over the coast on both sides of the Atlantic ocean. These animals live under rocks and stones on sandy sea beaches, at such a level as to be completely submerged twice a day by the tide. The eggs of this minute animal, itself only about three to four millimeters in length, are larger in proportion than those of any other members of the group whose eggs are as yet known and hence offer better advantages for study. A Frenchman, Lemoine, published an account of the external features of the eggs and some stages of the embryos of form allied to Anurida and announced that the cleavage was holoblastic and approximately equal. The investigations on Anurida confirmed this statement in every way and with the added help of serial sections some interesting points were made out.

The egg instead of having any of the forms already described as typical for insect eggs is strictly spherical and contains a considerable, but not a large, quantity of yelk. The first and second cleavage planes are vertical, and the third horizontal, as is usual in holoblastic cleavage. The cells mass together from the beginning, and the result is a solid morula instead of a hollow sphere surrounded by a single layer of cells. When the cells are reduced to a uniformly small size by rapid divisions a change takes place in the method of cleavage. (Fig. 2.) The blastomeres, which up to this point have been distinct from each other, about equal in size and containing approximately equal amounts of yelk, begin to lose their distinct outlines. The nuclei surrounded by small masses of protoplasm slowly migrate outward toward the surface of the egg. During the process the nuclei and their surrounding masses of protoplasm divide repeatedly, and ultimately a layer of cells covers the surface of the egg, forming a uniform blastoderm of rather large cells. As a final result, after continued divisions, two of the primary germ layers are clearly established, an outer one of uniformly small nuclei imbedded in a common layer of protoplasm and showing no separation into separate cells, the ectoderm, and an inner one close below the ectoderm, composed of larger nuclei, lying in an equally undivided layer of protoplasm, the mesoderm. Inside, scattered through the yelk, are cells that have two different destinies. The yelk, after the migration of the nuclei and their surrounding masses of protoplasm, loses its cleavage and becomes a solid mass, containing scattered nuclei. Secondary yelk cleavage never appears.

In Anurida, then, we find several interesting points that connect the curious type of cleavage found in the eggs of the Insecta and known as centrolecithal cleavage with the simpler holoblastic type. These facts are:

1. Holoblastic, nearly equal cleavage exists in the early stages.

2. At a later stage holoblastic division is lost and the formation of the blastoderm takes place by the migration to the surface of the nuclei, surrounded by small masses of protoplasm.

3. No secondary yelk cleavage takes place.

The existence of these transitional characters in an animal as lowly as Anurida, standing at the bottom of the great and specialised group of insects, is extremely significant. It points most clearly to the derived nature of the complex type of cleavage, characteristic of the group. It designates the holoblastic type as belonging to insect ancestors and helps by just so much to indicate possible lines of ancestry. Not only the cleavage, but other points which cannot be discussed here, as the absence of the embryonic envelopes, amnion and allantois, the presence of a series of membranes shed from the embryonic surface and the existence of a large glandular organ, similar to one of the many organs known as a "dorsal organ," lead to a closer alliance of the insect race with crustacean or myriapod ancestors.

One point is indeed settled, that the Apterygota show truly generalised characters and may be considered closely similar to the primitive insect; their lowly characters are not entirely due to degradation, but in part to direct inheritance and non-progression.

Returning to the question of cleavage, it is interesting to note among many of the arthropod groups transitional forms from the holoblastic to a more complex type of cleavage. In Korschelt's and Heider's text-book of embryology, the crustacea are classified according to their cleavage and a large group is made of those forms in which holoblastic cleavage exists at the beginning of development and a change comes in later. Brauer's figures are given for the crustacean Branchipus in which the change takes place in the following way: Holoblastic cleavage results in a distinct and regular central cleavage cavity. By repeated divisions a layer of small, narrow and much elongated columnar cells results, having the nuclei on the periphery and the long yelk-filled stems extending into the center. Eventually this inner yelk-laden part forms a fused mass, continuous, however, with the small outer blastoderm cells. (Fig. 3.) Among the Pantopoda there are two methods of cleavage, the one showing total cleavage at first, followed by a migration of all the cleavage nuclei to the periphery, with the ultimate obliteration of all cleavage planes in the yelk mass. Another type shows holoblastic cleavage up to the sixteen celled stage with the formation of a distinct central cavity. Later the entoderm is formed by delamination of the inner part of the cells, giving rise in this way to the inner germ layer by a method of multi-polar migration.

Among the myriapods purely centrolecithal cleavage prevails, accompanied by a fragmentation of the yelk mass, that from the surface strongly suggests holoblastic cleavage. The central nuclei finally migrate to the periphery along these lines of pseudo cleavage. (Fig. 4.)

These few facts show how wide-spread among arthropods are such changes during cleavage. But a passing reference can be made to the important bearing such changes have on the allied questions of development. This variation causes the inner germ layer or entoderm to be formed sometimes by invagination, sometimes by delamination and at others by the commonest method of cell migration from a definite point or points.

In this way the bearing of the question of the origin of the great primary germ layers is shown to be intimately connected with the form of cleavage prevailing in the development of the organism, and the value of any contribution on the point, however small, is indicated.

PLATE I.

Fig. 1. Typical insect cleavage.

Fig. 2. Anuridan cleavage.

Fig. 3 Crustacean cleavage.

Fig 4. Myriapod cleavage.